# THE LATERAL LINE SYSTEM OF SENSE ORGANS IN SOME AMERICAN AMPHIBIA, AND COMPARISON WITH THE DIPNOANS.

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The general structure of the individual sense organs is well known, and their distribution has been worked out for a considerable number of the Amphibia. The availability of many Urodeles, some of them important and isolated forms, as *Amphiuma* and *Siren*, led to a study of the distribution of the organs in eight of the tailed Amphibia on which nothing had been published, with the purpose of determining their presence and the plan of distribution. A comparison with the condition in the Dipnoans, *Lepidosiren* and *Protopterus* was made, and they were added to the Amphibia first studied. Most of the specimens studied were in the Museum of Vertebrate Zoölogy of Cornell University, and for the privilege of examining them I am indebted to Professor B. G. Wilder, Curator. Considerable material, also, belonging to Professor S. H. Gage was placed at my disposal by him, to whom also I am indebted for numerous suggestions and kindly interest in my work.

To the distinctive features of the Ichthyopsida, or fish-like vertebrates, enumerated by Huxley when he first pointed out the natural provinces in which the Vertebrata were grouped, there might be added, since 1876, that system of sense organs which, with the canals in which it is often enclosed, has been variously spoken of in the literature of science as the muciparous canals, lateral line system of sense organs, organs of a sixth sense, branchial sense organs, etc. It is but lately that the importance of these sense organs has begun to be fully estimated, and more careful observations have been made upon certain of the forms. The literature upon the subject is voluminous, but

despite the fact that so much has been written, except in the three or four most recent contributions, especially those of Ewart, '92, and Allis, '89, there has been no account of this system at all complete for any form. This is due largely to the fact that attention has been mainly confined to a study of the canals and their branches rather than the structure, distribution and innervation of the organs themselves—which is indeed very much like attempting to understand the oyster or snail from a study of its shell alone.

The first-recorded observations upon the system were made by Stenonis, in 1664, upon the canals in a species of skate. From that time the system attracted more or less attention. Lorenzini and Monro *secundus* may be mentioned as two of the more important early contributors. By most of the first writers the function of the system was regarded to be the secretion of mucus and its distribution over the body of the fish. Jacobson in 1813 first arrived at the conclusion that the system of canals constituted a sensory organ for the purpose of transmitting the vibrations of the water to the nerves, as he believed. However, it was not until Leydig in 1850 discovered the sense organs themselves and made microscopic examination of them that the step in the right direction was made, and a morphologic basis given for the theory of the sensory function of the system. His final and most complete account of the system appeared in 1868, upon the "Organs of a sixth sense" as he regarded them. Since 1813, among others who worked upon this system in fishes may be mentioned De Blainville, Robin, McDonnell, Schulze, Bodenstein, Solger, Wright, Fritsch, Beard, Garman, Allis, Guitel, Ewart, Pollard and Collinge; especially important are the researches of Allis, Guitel, Ewart and Pollard, by whom the distribution of the sense organs in the canals, their relation to the pores by which the canals communicate with the exterior, and the innervation, have been quite thoroughly worked up in the forms investigated by them, namely, *Amia*, *Lophius*, *Laemargus* and *Raia*; Pollard has also compared the distribution of the organs in five Nematognaths with a view of determining

their taxonomic value. Garman has studied the canals in many Elasmobranchs and in the Holocephala chiefly to ascertain their value in classification; for a more detailed account of the early literature of the subject and the views and results of the various writers Garman's paper should be consulted; upon this the above account of the early history of the subject is based.

Much still remains to be done on the system, especially among the Teleosts where there is a considerable variation in its development, which, in connection with the wide range in life-habits, may afford some clue to the function and importance of these sense organs. The modifications of the bones of the skull due to the presence of the canals and the possible bearing it may have on the origin of the vertebrate ear, demand that far more exhaustive study be bestowed upon them than has been up to the present. Particularly valuable will be careful and thorough investigations upon the early appearance and development of the system.

Merkel, in his monograph upon the nerve-terminations in the skin, recognized two classes of related cutaneous sense organs which he termed end-buds (Endknospen) and nerve-hillocks (Nervenhügel), and to the latter belong the organs of the lateral line system. For nerve-hillock, the monomym *neuromast* proposed by Wright is preferably employed.

The end-buds are found in fishes distributed in the skin, particularly of the head, and in the mouth cavity where, in the higher vertebrates, they appear as the taste-bulbs. They are situated upon papillæ of the cutis and are formed of long rod-like cells extending throughout the height of the bulb. In "fishes" they are always flush with the surface of the epithelium or even project beyond it. When situated in the skin they appear to be tactile organs; in the catfish the long barbels around the mouth appear to be little else than carriers of these sense organs (Wright).

With the neuromasts, on the other hand, there is a differentiation of certain of the cells, some of them being conical, pear-shaped and short, but bearing a more or less distinct bristle;

furthermore, the neuromasts evince a tendency to withdraw themselves from the surface. This tendency is carried to an extreme in the majority of "fishes" in which the lines of sense organs, which constitute the lateral line system proper, sink beneath the surface and occupy canals which open upon the skin by means of pores, generally between the sense organs. Complications may be yet increased by enclosures of the canals in bone, as if for protection, and the pores may become many times divided, producing seemingly the effect of still further withdrawal of the sense organs from the exterior. Examples of this last occur in *Amia* and the *Clupeidæ*. Again, in other forms, the organs of the lateral line system simply occupy pits in the epidermis, or are contained in an open groove; examples of each are *Lophius and Chimæra*.

In "fishes" the typical arrangement of the canals or lines is (1) one along the side of the trunk, causing the well-known lateral line. When scales and a canal are present it perforates each scale obliquely, and a sense organ and pore generally occur in each. The organs of this group are innervated by the lateral nerve, often spoken of as the lateral branch of the vagus. There are four lines on each side upon the head; (1) one above the eye, the supra-orbital, innervated by the ophthalmicus superficialis VII.; (2) below the eye, the infra-orbital, innervated by the buccal branch of the seventh nerve; (3) the mandibular or hyomandibular, upon the lower jaw, innervated by the hyomandibular branch of the seventh, and (4) a transverse line in the occipital region which meets its opposite, thus uniting the system on the two sides, and belongs to the lateral system. These lines may either be independent of each other or connected. Accessory lateral lines may be present, which in one genus (*Mugil*, McDonnell) reach the number of nine; lines of neuromasts may also be present in the skin of the head and trunk in addition to the typical lines, and a study of their distribution will doubtless afford a clue to the origin of the accessory lateral lines and explain departures from the type, which, because of their greater development, were more readily observed.

In 1861, eleven years after the sense organs in the canals of fishes had been discovered, Schulze, '61, reported the presence of homologous sense organs in branchiate Amphibia. In this class (the Amphibia) the neuromasts retain their simple primitive condition and remain in the skin, but slightly, if at all, withdrawn beneath the surface. Since the first discovery of these organs in Amphibia, there have been made, as far as I can ascertain, but half a dozen or so communications upon the subject by six investigators, namely, Leydig, Schulze, Langerhans, Bugnion, Malbranc and Wiedersheim. Leydig's more complete discussion is given in his last article to which I have not had access. Of the others Malbranc's paper is by far the most exhaustive, being a study of the structure and distributions of the sense organs in *Proteus*, *Menopoma*, *Triton*, *Salamandra* and *Salamandrina*, and the tadpoles of the anura *Bombinator*, *Pipa* and *Rana*. Wiedersheim makes the important statement that in *Amblystoma* and *Salamandrina* the sense organs become covered with epidermal cells during the period of terrestrial existence and are again uncovered when the life in the water is resumed. To the above should be added Cope,* who, though he evidently did not recognize the presence of this system of sense organs in the Amphibia, speaks of the depressions which mark the location of the organs as "mucous pores," and describes their location for a wide range of urodeles and has given figures showing the distribution in a number, which, however, since he does not recognize that they were more than "mucous pores," are often inadequate. There exist in the adult of *Salamandra*, which is a land form, "pores" upon the dorsal side of the head in the region of the so-called parotid gland of certain Amphibia, and upon the body in two rows, occupying in general much the same position as two of the lines in the sense organs did in the larva. They have nothing to do with them, however, but are the openings of glands. Apparently Cope regarded the "pores" which he found in so many forms as homologous with the gland openings in

* Of eleven general articles and books upon the Amphibia examined, in five only was the presence of this system noted.

*Salamandra*, and therefore termed them "mucous pores." * * It is also possible he may have had in mind the pores by which the canals in fishes opened upon the surface; the sensory nature of the system had been too long known to admit of their being spoken of as "mucous pores" were *pore* itself not inappropriate in Amphibia if used in the same sense as in fishes.

The original matter here consists mainly in a presentation of figures of the distribution of the organs in certain American urodeles and comparisons of them with each other and forms in which the distribution had been already investigated. Cope's descriptions will be used to supplement my own for forms in which the system exists and which have not been accessible. The purpose is to ascertain the presence of this system and determine what may be the typical distribution of the organs for Amphibia.

In examining the distribution in Amphibia a comparison with other Ichthyopsida is inevitable, and as far as possible the names which have been applied to the lines in "fishes" will be employed here. The only lines whose homology with those in teleosts, ganoids and elasmobranchs is unmistakable are the lateral lines and the lines above and below the eye, which are accordingly spoken of as the supra and infra-orbital lines respectively. The lines upon the side and venter of the head are not so easily compared. They are doubtless innervated by the same branch of the seventh (mental, Strong) and represent the hyomandibular canal

* * The close resemblance between the distribution of the sense organs in the larva and the "pores" in the adult *Salamandra*, caused Leydig to advance the rather remarkable theory that at transformation the sense organs became changed into large glands. Undoubtedly, however, the similarity in location is merely coincidence, and the sense organs in the larva perish and are at the time succeeded independently by the glands. Leydig's words are: "Nachdem geschwanzte und ungeschwanzte Batrachier aus Kiemenathmern zu Lungenathmern geworden sind, haben sich die Organe der Larven zu den grossen Hautdrüsen des Kopfes und der Seitenlinien umgebildet, welche auch jetz noch durch die Art des Secretes und dadurch, dass zahlreiche Nerven an die Gegenden, wo sie liegen, herantreten, von gewöhnlichen Hautdrüsen sich verschieden verhalten" (Malbranc).

system of fishes, with any associated lines of free neuromasts there may be. For convenience in description I shall use some locative terms employed by Garman in Elasmobranchs, even though it is not demonstrated at least, that the lines in the two classes are homologous, though occupying much the same regions.* They are therefore only provisional.

*Proteidæ.* Of the two existing genera of this family, *Proteus* of Europe has been studied by Bugnion and Malbranc; figures 1–3 and 16 show the distribution of the neuromasts in *Necturus*. Comparison of these two genera shows the conditions strikingly alike, the chief difference seeming to be due to the more elongated form of the head in *Proteus*. The organs in that genus are described by Bugnion as occurring in groups, occupying linear depressions in the epidermis. These groups again are associated together in lines or series upon the body. Bugnion recognized upon the lower jaw, "lignes divergentes," "series marginales," and between them "groupes obliques;" upon the side of the head groups which converge toward the corner of the mouth; upon the dorsal side of the head a line above the eye terminating in a cluster dorsad and cephalad of the prenares (groupe nasal anterieur), and also a cluster of groups caudad and ventrad of the nostril (groupe nasal et posterieur). In the occipital region of the head is an aggregation of groups which is continuous with the lateral line. A ventral line passes ventrad of the arms and terminates in the region of the legs. A dorsal corporal line of groups transverse to the long axis of the body was also recognized by Malbranc. The number of individual organs in each group varied from four to eight.

* The true homology of the lines, it is felt, is determinable by the nerve supply. Tested in this way, Ewart finds for the lines in Teleosts the following equivalents in Elasmobranchs, the canals of the latter being given as named by Garman: Infra-orbital=orbital, sub-orbital, orbito-nasal, nasal, half of median and prenasal canals; supra-orbital=cranial, rostral and sub-rostral; hyomandibular=angular, jugular, oral, sub-pleural and pleural. There exists the possibility that some of the lines in sharks represent lines of neuromasts existing free in the skin in the teleosts, which have not been recognized.

Though his figures show a very close resemblance, the less elongated head of *Necturus* permits a better idea of the arrangement. Upon the dorsum of the head in *Necturus* there exists caudad of each eye a cluster of groups which is divided into two lines, one of which passes dorsad, the other ventrad of the eye, the supra-orbital and infra-orbital lines. Fig. 2 requires but little supplementary description; many of the groups, especially cephalad of the eye, are oblique, and upon the snout their arrangement is as if radiating from a common center (Fig. 1). In the occipital region of the head is a triangle of groups continuous caudad with the lateral line; two or three groups form a short transverse series suggesting an occipital line. Upon the venter of the head (Fig. 3) are readily recognized the lines of Bugnion; lines of groups diverging from the corner of the lower lip toward the latero-caudal corner of the head, the gular lines, a line along the margin of the lower lip, which approaches the gular line at its cephalic end and will be spoken of as the oral line. Associated with the groups of these lines whose direction corresponds to that of the line are others which are transverse or oblique (groupes obliques of Bugnion). Upon the side of the head (Fig. 1) may be recognized (1) a line of somewhat oblique groups from the infra-orbital caudad of the angle of the mouth to the oral line; (2) a line of groups from the corner of the mouth to the caudal end of the gular line, and (3) a trend of groups from the throat where the gular line terminates caudally toward the infra-orbital, communicating also with the occipital group. These will be termed the angular, jugular and post-orbital lines or series respectively.

Upon the trunk the three lines are present. The lateral line is composed of longitudinal groups and extends from the occipital region nearly or quite to the end of the tail. The ventral line curves around ventrad of the arms and extends to the region of the vent; it is not continuous with any of the groups on the head. A dorsal line of transverse groups was present, though apparently weak. However, the tendency of the skin to form little transverse furrows and folds rendered it difficult to determine

the precise conditions existing; doubtless other groups in addition to those shown in the figure exist and were not detected. The organs in each group varied in number from six to eight.

*Cryptobranchidæ.* The distribution in *Cryptobranchus alleghaniensis* has been heretofore described and figured by both Malbranc and Cope, and my own observations can little more than add confirmation. In this form the organs open by circular or oblong pores upon elongated dermal papillæ (Fig. 40), which they thus divide into two, reminding one at once of the "Spalt-Papillen" of Fritsch in the ray, containing free neuromasts in the skin, and the papillæ in the skin of the lamprey which are similarly halved by a slit-like depression at the bottom of which a sense organ is situated.* Though the orifices are rarely oblong the tendency of the organ corresponding to the groups in *Necturus* is believed to be, as in the " Spalt-Papillen," transverse to the papillæ, and in the single diagram of the venter of the head introduced for comparison, this is so indicated by a short line (Fig. 40). This being the case, the tendency of the organs in *Cryptobranchus* and the direction of the groups in *Necturus* correspond.

The three corporal lines occur as follows: The dorsal line is weak and is represented by about ten or twelve transverse organs, and extends to about the level of the end of the abdomen. The ventral line contains about 36 organs; it extends from just cephalad of the legs, where it curves in toward the meson, to cephalad of the arms, passing ventrad of them and curving dorsad to end in a short transverse line. It occupies a position ventrad of the lateral fold present in *Cryptobranchus.* The lateral line lies just

* The distribution of these organs in *Petromyzon planeri* has been figured and described by Langerhans, who regards them, and correctly it is thought, as homologous with the lateral line sense organs. They are arranged in lines upon the head which are difficult to homologize with those in higher forms. Upon the body Langerhans recognizes dorsal, lateral and ventral lines, of which the first two are evident, the ventral is short and possibly may not be a corporeal line. The histologic structure of the organs in the Lamprey seems not to have received sufficiently accurate investigation, and on the nerve supply practically nothing has been done; it would offer an interesting and important, though rather difficult, research.

dorsad of this fold and extends to the tip of the tail. Upon the head it seems to connect with the post-orbital series.

Upon the ventrad aspect of the head the gular and oral lines are well developed, the latter covered for a portion of its distance by a labial fold. The former is accompanied by the usual transverse organs and extends upon and over the lateral fold upon the head. On the ventral side of this fold a double line of twelve or fourteen organs extend from the gular to the corner of the mouth (jugular). Upon the dorsal side of the fold there is a trend of organs cephalad to the orbital group, which appears to represent the post-orbital series. The eye is surrounded by the customary series of organs, which cephalad of it are so thickly placed that from the material at hand it was impossible to reduce them to a system. Some were parallel and some transverse or oblique to the assumed trend of the lines. An angular passing around the corner of the mouth to the oral was present.

Microscopic examination shows the neuromasts in *Cryptobranchus* much larger than in *Necturus*, though of the same typical structure; compared with *Necturus* they are also much fewer, one organ in *Cryptobranchus* more nearly representing a group in *Necturus*.

*Amblystomatidæ*. Of the genus *Amblystoma*, species *punctatum*, both larval and adult forms were examined and the distribution of the sense organs is given in Figs. 4–11, 17, 19, 33 and 36. *Amblystoma* appears in the relation of the groups to the lines to form a single exception to the type presented in the other urodeles examined, and for that reason and because the abundance of larval material rendered it a convenient form in which to illustrate it, the later development of the system in the larva is represented by Figs. 33, 4, 5, 19, 17, 10, 11 and 9. The questions and difficulties which involve a study of the first appearance and early development of the system render any treatment impossible here. The Amphibia also do not seem to afford as good opportunties for such an investigation as other Ichthyopsida.

The presence of the sense organs could be detected in yet unhatched larvæ. The distribution in a larva 16 mm. long is shown in Figs. 4, 5 and 19. Upon the dorsum of the head the supraorbital lines are readily seen and the groups in the occipital region also. A yet simpler arrangement is shown in Fig. 33 of a larva whose arms are just budding. Upon the venter of the head the oral and gular series are recognized with tendency to a transverse line just cephalad of the gular fold as in *Necturus* and *Cryptobranchus*. There are small accessory, doubtless developing, organs beside those forming the typical lines. Upon the side of the head (Fig. 19), are seen the infra-orbital, angular, oral and jugular, each consisting of few organs simply arranged. All three lines upon the body are present and presenting the typical arrangement; those in the lateral line were oblong as if exhibiting a tendency to transverse fission.

In a larva 28.5 mm. long (Figs. 10, 11 and 17), the system has reached a greater complexity and higher development, and in place of single organs occur groups of two or three, as in *Necturus*, though not marked by a depression. In the arrangement, however, there is a difference. While in *Necturus* and also in the other urodeles examined the groups in the lateral and ventral lines on the trunk, and generally the lines on the head, are parallel or nearly so with the lines in which they occur and transverse in the dorsal corporal line, in *Amblystoma* the condition is reversed and the small groups are transverse to the direction of the line in the ventral and lateral lines, and parallel or nearly so in the dorsal lines, etc., agreeing in this with the condition of the groups in the corporal lines in Anura larva (Malbranc and Fig. 37). Herein lies the most puzzling peculiarity of the distribution in *Amblystoma*. The general regions of location recognized before in *Necturus* are easily traced in the plottings.

The dorsal view of the head of an older larva introduced for comparison shows a yet greater development of organs and groups. In an axolotl 15 cm. long, Malbranc states that in the lateral lines the groups, which are as in *Amblystoma* transverse,

consist of as many as ten organs which are, however, oblong and their long axis parallel with the direction of the line.

In the adult *Amblystoma* the same arrangement occurs, though the apparent number of organs is much reduced. Figures 6–8 are plottings of an adult 18 cm. long. In many individuals taken in the Spring it is impossible to find more than a trace of the system, and in one the lines upon the head and the lateral and dorsal lines on the body were very distinct, but the ventral line was apparently missing; this is doubtless due to the fact, stated by Wiedersheim as quoted before, that in *Amblystoma* the sense organs become covered by epidermal cells when the animal assumes a terrestrial existence and again appear when it enters the water, a fact I can confirm, since, when no organs can be perceived from a superficial observation, sectioning reveals them in the epidermis, but concealed by overlying epidermal cells. Irregularity in the reappearence of the organs explains the apparent absence of certain lines, and though there is no positive evidence, I am inclined to believe that none of the organs disappear at transformation, but only a few reappear in the adult when the life becomes aquatic at the breeding season, the rest remaining concealed in the epidermis. In *Amblystoma* the lateral line terminates at about the level of the vent and a more dorsally situated line succeeds upon the tail. Malbranc regarded this as properly belonging to the lateral line rather than the dorsal, a view which is supported by the condition in other urodeles, notably *Dicmyctylus* and *Gyrinophilus*.

Beginning at about the level of the vent there are upon the dorsal surface of the tail on each side a row of some 60 or more openings occupying the line of the sense organs and resembling them greatly. These pores are oblong and transverse to the axis of the body, and in some instances there are two openings forming a transverse pair. Around each the pigment is absent from the skin, thus making them more distinct. At first the impression is strong that they are sense organs until dispelled by closer examination and sectioning of the skin which shows them to be gland openings. The sense organs may readily be detected

in their midst however. The condition illustrates how easily the two classes of openings may be confused and accounts for Leydig's wrong conclusions. Cope also did not recognize the difference.

Cope figures, p. 60, the sense "pores" upon the head in *A. punctatum* and describes them page 57. He also notes their presence in *A. conspersum, copeanum, jeffersonianum,* and in the allied genus *Chondrotus.*

*Plethodontidæ.* Cope describes and figures the distribution in *Stereochilus marginatus,* p. 153. His words are "the mucous pores on the head are distinct and large. They form a double series along the canthus rostralis and a single one above the orbit which turns round the latter behind and is continued below it and along the side of the muzzle to the nostril. A series of similar large pores extends along the middle of each side."

The system is distinct in *Gyrinophilus.* Figs. 18, 24–26 are of a larva of *Gyrinophilus porphyriticus* 82 mm. long. The supra-orbital line is but weakly developed, the organs being more abundant toward the nostrils. The infra-orbital is well represented and presents the characteristic radiating arrangement caudad of the prenares. Each organ is oblong and its location readily marked by the absence of pigment from around it. The oral line is well developed with 2–3 transverse organs accompanying it, corresponding to the groups in *Necturus.* The angular line is present and the jugular represented by 4–5 organs. The gular line is distinct though apparently weak near its middle. The postorbital group is well developed. The lateral line connects with a small occipital group on the head and extends to the tip of the tail, where the organs are more crowded and the line more dorsally located, as in *Amblystoma.* The dorsal line is represented by 12–15 transverse organs and does not reach the level of the hind legs. The ventral line is more strongly developed, but yet weak. The position is typical as seen from the figure (18), *Gyrinophilus* thus agrees closely with the general scheme of arrangement exemplified in the forms examined before. In the adult the neuromasts are present though the fact

is less easily recognized. Cope plots some of the organs in a larva 11 cm. long. (Pl. XLII. Fig. 1.)

That the system is present in *Spelerpes ruber* is evident from the words of Cope on page 172: "The eye is encircled by a series of pores. These extend anterior to those on the side of the head to the nostrils and are more crowded. The lower edge of the lower jaw is encircled by a single series of pores and there are two other series nearly straight which start from the point of the chin and diverge backwards." The last two are clearly those which I have designated as the gular lines; the orals of the two sides would seem to meet at the meson.

*Desmognathidæ*. In *Desmognathus* the system is weakly developed though present. An examination of the adult *D. fusca* shows diverging gular lines consisting of seven or eight organs each with accessory organs (2–3). The oral line is represented by but two or three organs. The infra-orbital line is the most developed and consists of about ten organs under the eye and cephalad of it. The supra-orbital is apparently almost wanting, consisting of two or three organs only. Upon the body the lateral and ventral lines are present, the organs being about one for each segment. Of the dorsal line no organ was detected. The conditions in *Desmognathus* render it often difficult to determine their presence from superficial examination, and no serial sections of the trunk have been made, so that possibly a few organs may represent the dorsal corporal line which were not detected.

Cope has recognized the presence of the "pores" in the species of this genus. He says: "The pores in *D. ochrophæa* are very difficult to observe. In a few specimens I have seen a few of those of the lower series; the upper I believe to be wanting." In *D. fusca* he finds "one well and one little developed lateral series of mucous pores." Of *Desmognathus nigra*: "The mucous pores are well developed, and the two lateral series are often distinct in alcoholic specimens by their white color; when they become dry they are difficult to observe. There are two rather distant gular series within the mandibular rami on each

side, and one on each side extending inwards and forwards from the gular plica. The superior lateral series extends from the orbit to near the end of the tail; the inferior round the humeri to each side the pectoral region."

*Pleurodelidæ.* In the adult of *Diemyctylus viridescens* the depressions marking the location of the organs are very distinct. Upon the head the supra-orbital and infra-orbital series are well developed. In many the pores cephalad of the eye are oblong and exhibit the same radiating arrangement shown by the groups of organs in *Necturus*. Upon the side of the head are distinct the jugular and angular lines, and post-orbital group, which, however, does not seem to have any marked trend. The gular line starting from the caudal end of the jugular is formed of two series of organs, the more lateral of which are often transversely oblong, representing doubtless the transverse groups in *Necturus* and other forms. At its cephalic end it approaches the oral line which consists of some half a dozen or more organs. Upon the body the three lines are well developed, and in them the organs are associated into groups of two or three (Fig. 20). Of these the lateral line is as usual best developed, and caudad of the vent curves dorsad to occupy a position along the base of the caudal fin; it is not closely connected with the occipital group on the head. The dorsal line, in which the groups are transverse to the long axis of the body, runs out just caudad of the vent upon the caudal fin. The ventral line (Figs. 20 and 21), curves mesad beneath the humeri, cephalad upon the pectoral region, and likewise at its caudal end just cephalad of the legs, having thus its typical position and extent.

In the well advanced larva the conditions are very much as in the adult. For comparison a figure showing the distribution upon the dorsum of the head is given (Fig. 23). The lateral lines are very distinctly located by the absence of pigment from around the sense organs.

*Diemyctylus viridescens*, whose life-history has been worked out by Gage, passes through a period of terrestrial existence intermediate between the aquatic larval and adult stages, and there-

fore affords an excellent example of the forms, such as *Salamandrina* and *Amblystoma*, in which the sense organs persist and live over the time of life on land by being covered with epidermal cells, reappearing again when the aquatic life is resumed. The skin during the land stage is of a red color and rough with numerous horny papillæ. Examination of the skin or the exuvium with a lens fails to detect any of the orifices so conspicuous in the olivaceous, smooth-skinned aquatic adult. Examination of sections of the skin from the right regions demonstrates their existence, and there is no doubt that the sense organs persist from larva to adult covered, or nearly covered (as in the one figured, Fig. 34), by epithelium cells.

Comparison of the distribution of the sense organs in this form with European newts of this family, that have been examined by Malbranc, shows a very close resemblance. Cope has noted the presence and distribution of the pores in the other American species of this genus, *D. torosus* (p. 204).

*Amphiumidæ*. An alcoholic specimen of *Amphiuma means* was examined and this was supplemented by fragmentary observation of a living individual in which the location of the neuromasts was easily detected. The organs are in small groups of two or three each, which are indicated upon the figures by short lines. A comparison of the figures with those showing the distribution in other genera indicates how closely *Amphiuma* conforms to the typical amphibian arrangement. The supra-orbital and infra-orbital lines are well developed, the former extending some distance caudad of the eye. In connection with each line are numerous groups which are transverse or oblique to the direction of the main lines, especially cephalad of the eye, recalling the relations in *Necturus*. The lateral line extends cephalad upon the head, curving ventrad toward the post-orbital groups as in *Necturus*, and not connecting with the orbital lines. Upon the venter of the head the arrangement of the lines is almost diagrammatic. Both oral and gular lines are well developed and in connection with each are the numerous transverse groups which have been found so often before. Upon the

side of the head are quite distinct jugular and post-orbital lines, the former extending from the angle of the mouth to the caudal termination of the gular; the latter, from the infra-orbital, of which it appears as a caudal continuation, to the meeting of the gular and jugular.

Although Cope states that no distinct rows of pores exist on the body, the examination of the living specimen showed clearly the presence of all three lines, the lateral extending throughout the length of the elongated body, the ventral terminating in the region of the vent, and the dorsal much more weakly developed. The cephalic ends of all three lines are shown in Fig. 13. Cope's description of the mucous pores upon the head agrees in the main with the figures.

It was not always possible to determine how many neuromasts occurred in each group; where observed, the number was only two or three, and uniformity in the size of the groups rendered it probable that the latter number was not exceeded. Where the organs were apparently single, a dot was employed to represent their location.

*Sirenidæ.* Four small alcoholic individuals of the genus *Siren* were examined, and though the condition of the epidermis made it impossible to give the system a thorough examination and make complete plottings, Figs. 30 and 31 suffice to indicate that the neuromasts exist and that they conform in their distribution to the general scheme in Amphibia. Upon the trunk three lateral lines occur and their position and extent are entirely typical. Wherever the condition of the epidermis rendered the number determinable, the small groups which were found contained two organs each. They are longitudinal in the lateral and ventral, and transverse in the dorsal line. The relation of the cephalic and caudal ends of the ventral line to the axilla and vent is shown by Fig. 31 and is typical, resembling the condition with forms in which hind legs are present.

Upon the head it was difficult to determine more than the rich abundance of the neuromasts, in the usual regions. Upon the venter of the head the gula line is well developed (Fig. 30),

and the arrangement of groups complicated. The presence of oral, angular and jugular series could not be determined because of the ill preservation of the epidermis.

*Anura.* But little attention has been paid to the system in the tailless Amphibia. For comparison merely, the distribution in a species of *Rana*, probably *catesbiana*, is given (Figs. 37 and 38). The existence of the neuromasts in many of the European genera has been determined by Schulze, Leydig and Malbranc,* though, as far as ascertained, only of *Bombinator* and *Rana* have figures been published showing the distribution.

In *Rana* three lateral lines are readily seen, the dorsal meeting the lateral at its cephalic end. The orbital lines are well developed and encircle the prenares also. The ventral line extends from the region of the vent making a curve dorsad around the region where the arm is concealed and is continuous apparently with a transverse line (Fig. 37). When in later larval life the arm appears, the line passes dorsad of it instead of ventrad as in the urodela, a rather noteworthy difference apparently unobserved hitherto. Another difference between the two groups, constant for all forms examined except *Amblystoma*, was noted by Malbranc; it is that while in the tailed Amphibia the linear groups of neuromasts are longitudinal in the lateral and ventral lines, and transverse in the dorsal, in the tailless forms the relation of group to line is exactly reversed and the groups are longitudinal in the dorsal, and transverse in the lateral and ventral lines. In the orbital lines also the groups are transverse or nearly so, especially near the eye.

It is interesting to note the existence (Malbranc) of the sense organ in a larva of *Pipa dorsigera*, 2.5 cm. long, taken from the back of the mother.

DIPNOANS.

When it was desired to compare the system in Amphibia and

* Schulze examined *Bombinator igneus*, *Rana esculenta*, and *temporaria*, *Pelobates fusca* and *Hyla arborea*; Leydig, *Bufo cinereus* and *calamita*; Malbranc, *Bombinator*, *Pipa* and *Rana*. (Malbranc.)

in the Dipnoi, the only statements* upon the lateral line system in that group that could be found were so unsatisfactory that an examination of individual specimens was necessary.

Upon the system in *Protopterus* the most detailed account was given by W. N. Parker, who is quoted by Wiedersheim. He states that the organs are not confined to the lateral line, but occur dorsad as well as ventrad of it; that they are especially numerous upon the snout where they occupy grooves in the skin, and occur always free in the skin as in Amphibia and the young of many fishes.† His rather general statement needs supplementation and correction in several particulars. From the examination of five well preserved specimens, Figures 12, 27–29 were constructed, and the following may be said in discussion of them. As stated by Parker, the neuromasts are situated (in most of the regions) free in the skin, and not in canals as in most "fishes," and occur in the lines on the trunk, in linear groups of from four to ten organs each. Three lines are present upon the body as in Amphibia—dorsal, ventral and lateral. The ventral line arises ventrad of the gill slit, passes ventrad of the pectoral fin to the pelvic fin where it is interrupted, turning slightly dorsad instead of ventrad as in Amphibia, to be continued upon the tail by a line of rather long groups. The dorsal line is more weakly

* For the opportunity of consulting the Dipnoan specimens and literature I am indebted to Prof. B. G. Wilder.

† "Diese (Hautsinnesorgane) weichen in ihrem Bau von dem gewöhnlichen Verhalten bei Fischen und Amphibien nicht ab. Sie sind nicht allein auf die Seitenlinie beschränkt, sondern finden sich auch am übrigen Körper und zwar dorsal- wie ventralwärts. Ob es sich aber an diesen Stellen um eine regelmässige Anordnung handelt, vermag ich vorderhand nicht sicher zu sagen. Am Kopf, wie namentlich an der Schnauze, sitzen sie ungleich zahlreicher; dabei liegen sie auf dem Grund von grubigen Hauteinsenkungen, welch letzere man schon mit unbewaffnetem Auge erkennen kann. Es handelt sich aber nicht etwa um eine Betheiligung der Kopfknochen, d. h. letzere bilden nirgends schützende Furchen und Canäle. Dasselbe gilt auch für die im Bereich der Seitenlinie sitzenden Organe. Auch sie werden keineswegs von den Schuppen überlagert. *Kurz, allerorts sitzen die Hautsinnesorgane des Protopterus frei im Niveau der Epidermis,* ein Verhalten, welches mit dem der wasserlebenden Amphibien und den Jugendstadien sehr vieler Fische übereinstimmt." Parker, p. 7.

developed. The general direction of the groups composing it is longitudinal, although those in its cephalic part are somewhat oblique. The lateral line is composed of linear groups closely associated together. Upon the tail it either terminates some distance from the end or shifts its position, as is more probable, and is continued farther ventrad. Upon the head it is continuous with the orbital lines.

Cephalad of two transverse spurs in the occipital region, the continuation of the lateral line becomes enclosed within a canal which opens by three pores, as indicated in the figures, and forks at the fourth. The dorsal branch is continued above the eye as the supra-orbital line. After a series of eight pores, the line again occupies an open groove, succeeded by a short canal with three cephalad pores, of which the organs are again situated in a furrow in the skin.

The ventral branch passes through a canal with seven pores, where the infra-orbital line arises as a line of organs situated in a groove, the canal bending ventrad to be succeeded at the eighth pore by a line of organs occupying a groove along the edge of the lower lip, or the oral line. From its most caudal pore extends a line of neuromasts caudo-ventrad to meet another line upon the ventral surface of the head. They may be spoken of as the jugular and gular, and their relations are seen in Figs. 27 and 29. In addition to these main lines the accessory lines occur upon the head as shown in the figures.

As far as I can ascertain the only descriptions of the lateral line system in *Lepidosiren* were those of its discoverer, Natterer*

* "Diese Schleimkanäle beginnen an der Spitze der Schnauze und bilden jederseits zwei wellenförmige, mehrere Zweige aussendende Linien, deren sich eine oberhalb, die andere unterhalb des Auges, bis gegen das Hinterhaupt hinzieht, wo sie sich wieder vereinigen, zwei gerade gegen das Hinterhaupt aufsteigende Aestchen aussenden und von der Kiemenspalte an in gerader Richtung längs den Seiten des Körpers bis zum Schwanzende, analog der Seitenlinie der Fische, verlaufen. Die untere dieser wellenförmigen Linien gibt vor ihrer Vereinigung am Mundwinkel einen Zweig zum Unterkiefer ab, der den Kiefer umsäumet, sich von der Spitze desselben in einem doppelten Aste gegen die Kehle wendet, das Unterkinn begrenzet und von da in wellenförmigen Windungen die Kehle durchzieht

and Hyrtl,** when the system had not yet been discovered in Amphibia and was regarded as a mucus-secreting organ in "fishes." However, the comparison of their descriptions and the figure of Natterer, supplemented by the examination of a specimen in the Museum of Vertebrate Zoölogy of Cornell University, from which figures 43 and 44 were made, suffices to show that the distribution in *Protopterus* and *Lepidosiren* are very closely comparable, almost identical; that in *Lepidosiren* the neuromasts occur free in the skin, and no portion of the system, as in *Protopterus*, occupies canals. From the description of Natterer the presence of the ventral and lateral lines is evident, and I doubt not that the dorsal line is also present. The poor state of preservation of the epidermis in *Lepidosiren* did not permit my ascertaining its existence.

In *Ceratodus* the system is enclosed in canals, and the relation of the lines could not be determined from superficial examination. The lateral canal is the only one upon the trunk, perforating each scale and opening upon each by a trifid or quad-

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und dieselbe in mehrere Felder theilt, sich dann aber in vollkommen gerader Richtung zu beiden Seiten des Bauches dicht über die Hinterfüsse hinweg, längs der Basis der unteren Schwanzflosse bis an's Schwanzende, erstreckt. Die obere sendet einen Zweig wellenförmig quer über den Scheitel." Natterer, '45, p. 5.

** "Ein der Classe der Fische eigenthümliches und bisher bei keinem Amphibium beobachtetes System von Schleimcanälen findet sich unter folgenden Verhältnissen: Die Seitenlinie theilt sich, nachdem sie die ganze Länge des Stammes durchlaufen und über der Kiemenöffnung zwei convergirende Aeste gegen den Nacken abgegeben hat, hinter und über dem Mundwinkel in zwei Zweige, welche schlangenförmig gewunden über und unter dem Auge gegen die Schnauze ziehen, und am Lippensaum, zwei Linien von einander entfernt, endigen. Der untere derselben schickt gleich nach seinem Ursprunge drei Aeste zum Unterkinn, welche in der Mittellinie in einander überzugehen scheinen, and durch mehrere gewundene Zwischenschenkel mit einander communiciren, wodurch kleinere unregelmässige Facetten gebildet werden. Der obere hängt mit dem der anderen Seite durch einen über den Scheitel weggehenden Verbindungsarm, und ein Zoll hinter diesem, durch einen zweiten ähnlichen, zusammen. . . . . Die Verbreitung dieser Linien am Kopfe stimmt mit jener bei *Chimœra* vollkommen überein." Hyrtl, '45, p. 6.

rifid pore. Whether the ventral and dorsal lines were present as series of free neuromasts could not be determined.

Comparing the system in *Protopterus* with that in urodeles, resemblances appear in the presence of three corporal lines occupying the same relative positions as in Amphibia, the presence of lines on the head apparently representing the oral, jugular and gular lines in Amphibia, connected with the infra-orbital. Differences in detail in the two groups are manifest; most conspicuous is the apparent fusion for a part of their length of the infra-orbital and jugular, and the absence of an angular line.

In degrees of complexity of the system the three dipnoans stand, *Lepidosiren*, *Protopterus* and *Ceratodus*. In the first the entire system is superficial; in *Ceratodus* it is sunk in canals (except perhaps dorsal and ventral lines and accessory groups); while in *Protopterus* it is intermediate, a small portion only occupying canals.

HISTOLOGIC STRUCTURE OF THE NEUROMASTS.

In structure, as has been suggested before, the neuromasts in Amphibia are but little modified from the typical form. They are situated in the epidermis, but little if at all withdrawn from the surface and present throughout the class the same histologic structure. The following description is based upon the statements of Malbranc and my own observations:

The two kinds of cells are readily distinguished, the conical, pear-shaped or so-called sensory cells, and the spindle or sustentacular cells. The former occupy the center of the bulb extending only partly through its height. In number they vary from only a few to forty or so, according to the size of the neuromast. The nucleus is generally large, round and clear, possessing a small amount of chromatin. The cell-body, further, blackens somewhat on the application of osmic acid, though not so markedly as in the neuromasts of fishes. The ectal end of the cell bears a refractive bristle which in the larva is generally quite long; in the adult it is short, reaching, however, the free surface of the bulb. The ental or basal end which contains the nucleus seems generally to terminate bluntly; often

however, delicate varicose processes are to be observed. (Malbranc).*

Surrounding these is an enveloping sheath of long spindle cells which extend throughout the height of the bulb, their form being modified according to the shape and position of the surrounding cells.

The nucleus is generally situated near the basal or ental end which terminates in a number of delicate processes. Isolated cells of the two kinds from *Diemyctylus* are shown in Figs. 42 and 43; for comparison also are figured the neuromasts in *Necturus*, *Diemyctylus* and two developing (?) organs in *Amblystoma* in which the typical histologic structure is readily seen. The neuromasts in *Necturus* are the more withdrawn from the surface. The precise mode of termination of the nerve fibers in the neuromasts still demands attention, possibly for the determination of the value of certain theories.

GENERAL REMARKS.

The Amphibia afford in certain respects peculiar opportunities for the study of a sensory system associated with existence in the water. This is due to the fact that there are here included forms purely aquatic and forms as purely terrestrial in their habits of life, and yet others which spend a portion of their life in the water and a portion of it on land. In every family of the tailed Amphibia native in the United States the system has been found, and in five families of the tailless Amphibia. Since Malbranc has found the sense organs in a larval *Pipa*, and Leydig in a larva of the viviparous *Salamandra atra* taken from the oviduct of the mother, doubtless the system will be found in a more or less perfect state of development in all Amphibia at some period in their life-history. The genus *Plethodon* would be a good test form for determining this, since it is said at no period of its

*** Schulze has stated that these cells are directly continuous with nerve fibers. This last is improbable; doubtless the application of modern methods would show that such is not the case; it is important, however, since in that case these would be true nerve cells in the second modified epidermal cells.**

development to live in the water. In order to ascertain it possible the presence of the neuromasts in this genus, I examined serial sections through the head of a well developed *Plethodon erythronotus* embryo almost ready to hatch, but could detect no certain trace of the sense organs. However, if larvæ just hatched are examined, it is confidently expected that the organs will be found.

In the urodela the distribution may readily be reduced to the following type: Upon the body, three lines, a *lateral* continuous or not continuous with an occipital group, though not continuous with the orbital lines; a *ventral* line extending from under the arms in the pectoral region to near the hind legs; a *dorsal* line somewhat closely connected with the lateral at its cephalic end and seldom extending as far as the level of the vent. Upon the head, a series extending from behind the eye, above and below it to the snout, the *supra-* and *infra-orbital* lines; a line upon the lower lip, the *oral*, connected with the infra-orbital by the *angular;* a line from the angle of the mouth to the lateral corner of the head and there meeting a diverging line upon the ventral side of the head, and, when this is sufficiently developed, a line or trend of organs upon the side of the head; these the *jugular*, *gular* and *postorbital* lines of the descriptions and figures.

Comparison with other Ichthyopsida may not be of much value; however, the distribution approaches most nearly that in the Dipnoans, then in Elasmobranchs; among the latter *Chlamydoselachus*, apparently, in the greater extent of the gular line, shows most resemblance to the Amphibia.

In the tailless forms there are three corporal lines, the lateral and dorsal converging cephalad; also well developed orbital lines, and upon the ventral side of the head a line in the position of the oral and jugular, possibly representing both, and two transverse lines, with a possible gular. The changed form of body in the two groups renders a comparison difficult; it should be based on nerve supply. The curious difference in the relations of the groups in the lines upon the trunk in the anura and urodela has been noted before.

The significance of the arrangement into groups is apparent when the system is examined in the larva at different periods of development. Evidently as has already been maintained by Malbranc, each group sprang from a single organ by repeated fission in the same plane. His figures and my own observations clearly show that such is the case, as illustrated by Fig. 45. Exactly how this takes place, however, is unknown. Whether the sensory cells may arise from the supportive cells, or from sensory cells alone, and supported from supporting cells or from ordinary epidermal cells, yet awaits solution.

It is probable that the sensory cells alone determine the size, shape and division of the neuromast, and multiply by the division of previous sensory cells. In only one instance a karyokinetic figure was observed in a nucleus apparently of a sensory cell. The causes determining the plane in which fission takes place must be closely connected with the function of the sense organs, whatever it may be. Malbranc called attention to the often recurring arrangement of groups upon two coordinates perpendicular to each other, or nearly so (as in the gular line), pointing out the physical advantage in such an arrangement in perceiving the direction and strength of a vibration in the water, should such be their function. In Ichthyopsida, in which the sense organs are deeply sunken in canals, the pores often become many times divided. In *Amia*, Allis found that the primitive pores divide quite regularly in a certain plane for a number of times; these secondary pores again often divide in a plane at an angle to the first, generally a right angle or nearly so, reminding us of the groups in Amphibia. In forms, then, in which the sense organs are confined in canals, this division of the pores would seem to represent a potential division of the sense organs, which in forms in which the sense organs are freely situated, as in Amphibia, can be actual. It does not appear that any physiological experiments have ever been undertaken to attempt to ascertain the function and value of the system, nor are there as yet data for a comparison of the development of the system in different Ichthyopsida with their habits and form, from which some idea

might be obtained. Of the theories advanced, the facts of arrangement and development seems to render most reasonable the one of Jacobson, viz., that it is the perception of vibrations of the water, and that the distribution, and therefore multiplication of the organs may, perhaps, be to a certain extent regulated by and modified in accordance with mechanical advantages arising out of the form and habits of the animal.

In connection with the development of the individual sense organs should be mentioned the existence in *Cryptobranchus*, as observed by Malbranc and by the writer, of small organs in the skin which are covered with epidermal cells, and which he regarded as developing organs, which later break through the epidermis. This mode of development has been shown by Allis to exist in *Amia*. However, I do not consider it necessarily the proper explanation of these hidden organs in *Cryptobranchus*. They were also observed in the skin from the parotid region of an adult *Amblystoma* (the only region examined); in a very limited area, about five mm. square, were found two groups of two each, and one of three of these small submerged neuromasts. From the fact that the organs in the larva are more abundant apparently than in the adult, it is suggested that these are but supernumerary organs which do not appear in the adult, or do so subsequently when needed.

This calls the attention to the necessity, imposed by the life habits of certain urodeles, *e. g.*, *Diemyctylus*, for the neuromasts to live over a period of terrestrial existence, which is accomplished by the protection of the organs by a growth of epidermal cells. Doubtless this is also true for many other forms of semi-aquatic habits of life, *e. g.*, *Desmognathus*. In certain other urodeles, *e. g.*, *Salamandra*, and I believe *Plethodon* (if they exist at any time), the system perishes entirely in the adult. This is also the case apparently in all the Anura, though in *Rana* it persists until after both legs and arms are well developed and the tail has begun to be absorbed. There would seem, then, to be something other than an aquatic existence necessary for the maintainance of the neuromasts, since *Rana catesbiana* is more purely aquatic than

several of the Salamanders in which the system persists. Of the mode of final disappearance nothing is known.

The nerve supply of the system has never been worked out for Amphibia with sufficient completeness so that the innervation of all the various individual series is not definitely known. The investigations of Ewart and Strong, the latter upon the cranial nerves in the tadpole, have shown that in Amphibia and Elasmobranchs, at least, the nerves supplying this system arise just cephalad and caudad of the eighth nerve. In Urodela, at the level of the seventh, a nerve arises which divides, one branch becoming associated with the Gasserian ganglion of the fifth, and giving rise to the buccal and *opthalmicus superficialis VII.*, which, undoubtedly, supply the infra—and supra-orbital lines. The second branch joins the seventh and forms the mental (Strong) nerve which supplies the lines upon the ventral side of the head, and probably also the jugular and post-orbital lines. The lateral nerve arises just cephalad of the ninth and divides into three branches, the more dorsal much the smaller, which supply the group in the occipital region of the head and the three lines upon the body. As far as it has been possible to make comparative study the results sustain Strong. In *Necturus*, *Amblystoma* and *Diemyctylus* the roots described by him as innervating the lateral line system above, were all recognized and were in relative size quite proportional to the development of the system. In *Desmognathus* the roots arose so close to the seventh and ninth nerve that they were not readily distinguishable; however, the customary branch to the Gasserian ganglion was present, though very small, as it should be. In *Plethodon* I was unable to detect it, and believe the lateral line roots lacking.*

* Pinkus '95 has examined the larvæ of *Salamandra maculosa* and *atra*, *Desmognathus fusca and Salamandrina* and finds the lateral line roots as described by Strong. In the adult *Salamandra atra* and *Geotriton fuscus* the nerves are absent although in *Salamandra* a small strand of fibers passed from the seventh to the Gasserian ganglion, there to end without any corresponding issuing nerves. In *Protopterus* he found the lateral line nerves much as in the Amphibia. As would be expected from the distri-

Especially interesting and prominently advanced of late is the theory of the origin of the ear from this system of sense organs. In support of this are (1) the fact of the origin of the nerves supplying the neuromasts from the immediate neighborhood of the eighth, caudad and cephalad of it; (2) the general resemblance between the sensory cells and the hair cells of the ear; (3) the tendency of the neuromasts to sink below the surface in development, as does the ear; and (4) the embryologic evidence so far accumulated indicates that in fishes the ear and the lateral line system develop from a common epibranchial thickening of the ectoderm, which spreads caudad and cephalad to constitute the lines of neuromasts.

Despite the plausibility and attractiveness of the theory, its acceptance, it seems, should be held in abeyance until one or two points are determined. Ayers, who is one of the most ardent supporters of the theory, in the latest publication upon the relation of the nerve fibers and hair cells in the ear, states that cell and fiber are directly continuous and the nerve fiber does not terminate freely among them as had been held hitherto. This makes the hair cells true nerve cells, parts (one-half or less) of nerve units, comparable therefore to the sensory cells of the nose. On the other hand, the only application known to me of the impregnation methods (Retzius '93) indicates that in the neuromasts the termination of the fiber is free in an end brush, as it is in the end buds. This would make the sensory cells of the neuromasts but modified epidermal cells, and not comparable (if both Retzius and Ayers are correct) to the hair cells of the ear, which would be the morphological representatives (in part) of the nerve cells of the ganglia in connection with the nerves of the system. Therefore it is felt that the mode of termination of the nerve fibers in both the maculæ of the ear and in the neuromasts should be reinvestigated before the other facts are accepted in support of the theory.

bution of the neuromasts, the lateral nerve divides into three superficial branches, a ventral, lateral and dorsal, and a deep lateral one (*R. lateralis profundis*), which he describes as innervating the caudal portion of the tail (the caudal more ventral series of neuromasts).

METHODS.

The methods employed were of the simplest. Much of the material was alcoholic which had been previously prepared for museum purposes. Such forms as were available fresh, *e. g.*, *Diemyctylus*, *Necturus*, etc., were carefully killed in weak (one-third per cent.) chromic acid with ether, and the epidermis was then immediately examined with a lens, and the location and arrangement of the neuromasts ascertained; in *Necturus* they were difficult to detect in specimens less carefully treated. The larval *Amblystomas* were killed in either chromic acid (one-third per cent.) or platinum chlorid (one-quarter per cent.) and preserved in alcohol, and examined by strong reflected light with the compound microscope. Tissue for the histologic examination of the sense organs was fixed in Picro-aceto-sublimate. (Formula: fifty per cent. alcohol, 1000cc.; mercuric chlorid, five grams; picric acid, one gram; glacial acetic acid, 10cc.). The stains employed were Gage's hematoxylin and eosin, the last in an alcoholic (sixy-seven per cent.) solution. Collodion was used in imbedding and the blocks were cleared in Fish's Castor-thyme oil mixture. (Fish, 3.)

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## EXPLANATION OF THE PLATES.

The specimens from which most of the outline plottings were made were alcoholic, so that in many cases the shape and position of the legs and arms are unnatural.

Figures 1–3, 6–8, 16, 18, 20–22, 24–26, 30 and 31 were outlined at the required magnification by means of a vertical photographic camera. The specimens, in water or alcohol, were placed in direct sunlight, and in place of the ground-glass screen, a clear glass was used across which tissue paper was stretched and fastened, whereon the outline and as many details as were necessary were traced.

Figures 4, 5, 9–11, 17, 19–23, 33 and 36 were drawn with a compound microscope by the aid of an Abbe camera lucida.

From the curvature of the surface the relative position of sense organs at the periphery of any aspect would be falsely shown, hence, in many of the figures they were discarded and only the groups strictly belonging to any one aspect shown. The approximate magnification is given for each figure.

The names that have been applied in description to each line or series are indicated in the figures by the following abbreviations:

SO. = Supra-Orbital.
IO. = Infra-Orbital.
PO. = Post-Orbital.
J. = Jugular.
G. = Gular.
OC. = Occipital Group.
O. = Oral.
A. = Angular.
V. = Ventral.
D. = Dorsal.
L. = Lateral.

### PLATE I.

*Necturus maculatus.*

FIG. 1. Lateral aspect of the head; the short lines represent linear groups of 6–2 organs each, × 1.

FIG. 2. Dorsal aspect of head, × 1.

FIG. 3. Ventral aspect of head, × 1.

*Amblystoma punctatum.*

FIG. 4. Larva 16 mm. long. Ventral aspect of head, × 8; each circle in this and the following figures represents a sense organ.

FIG. 5. Larva 16 mm. long. Dorsal aspect of the head, × 8.

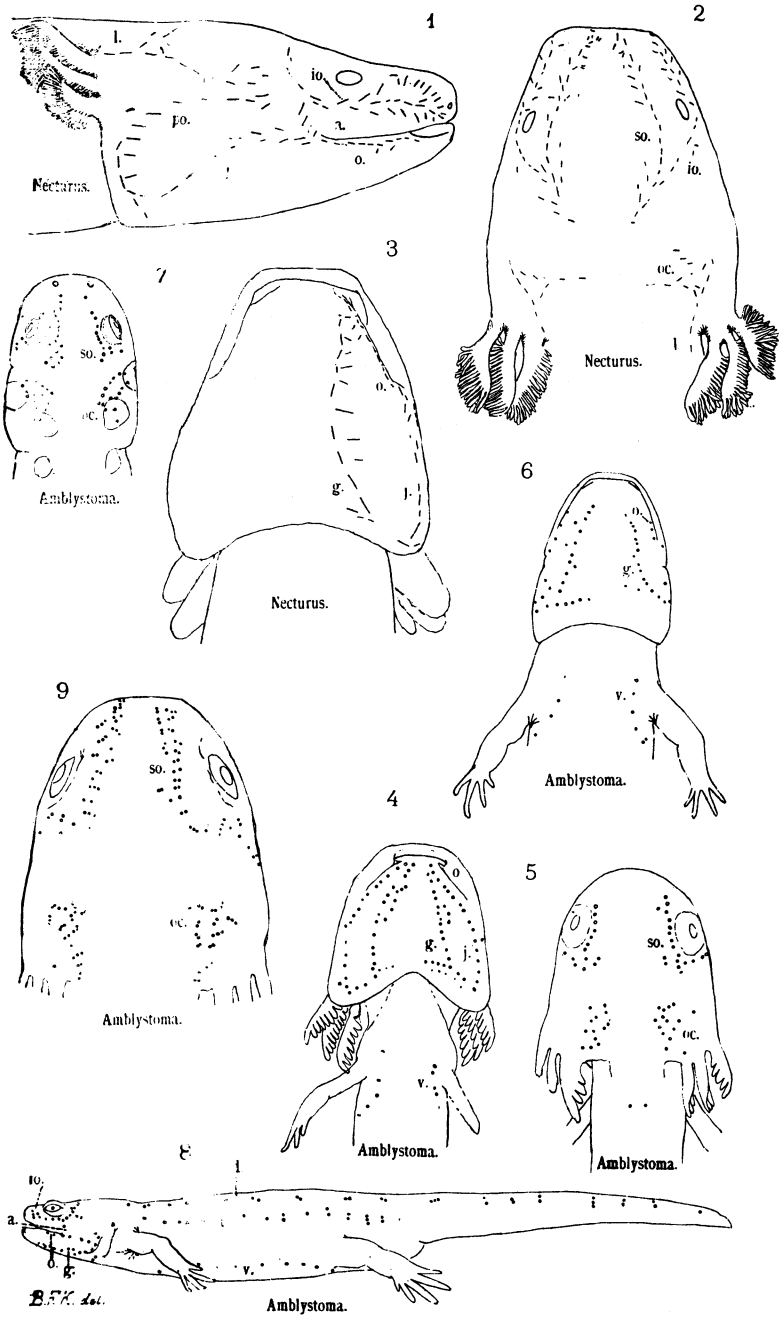
FIG. 6. Adult 18.5 cm. long. Ventral aspect of the head, × 1.

FIG. 7. Same. Dorsal aspect of the head, × 1.

FIG. 8. Same. Lateral aspect, × ½.

FIG. 9. Larva 52 mm. long. Dorsal aspect of the head, × 4.

# PLATE I.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Amblystoma.

## PLATE II.

*Amblystoma punctatum.*

FIG. 10. Larva 28.5 mm. long. Dorsal aspect of the head, × 8.
FIG. 11. Same. Ventral aspect of the head, × 8.

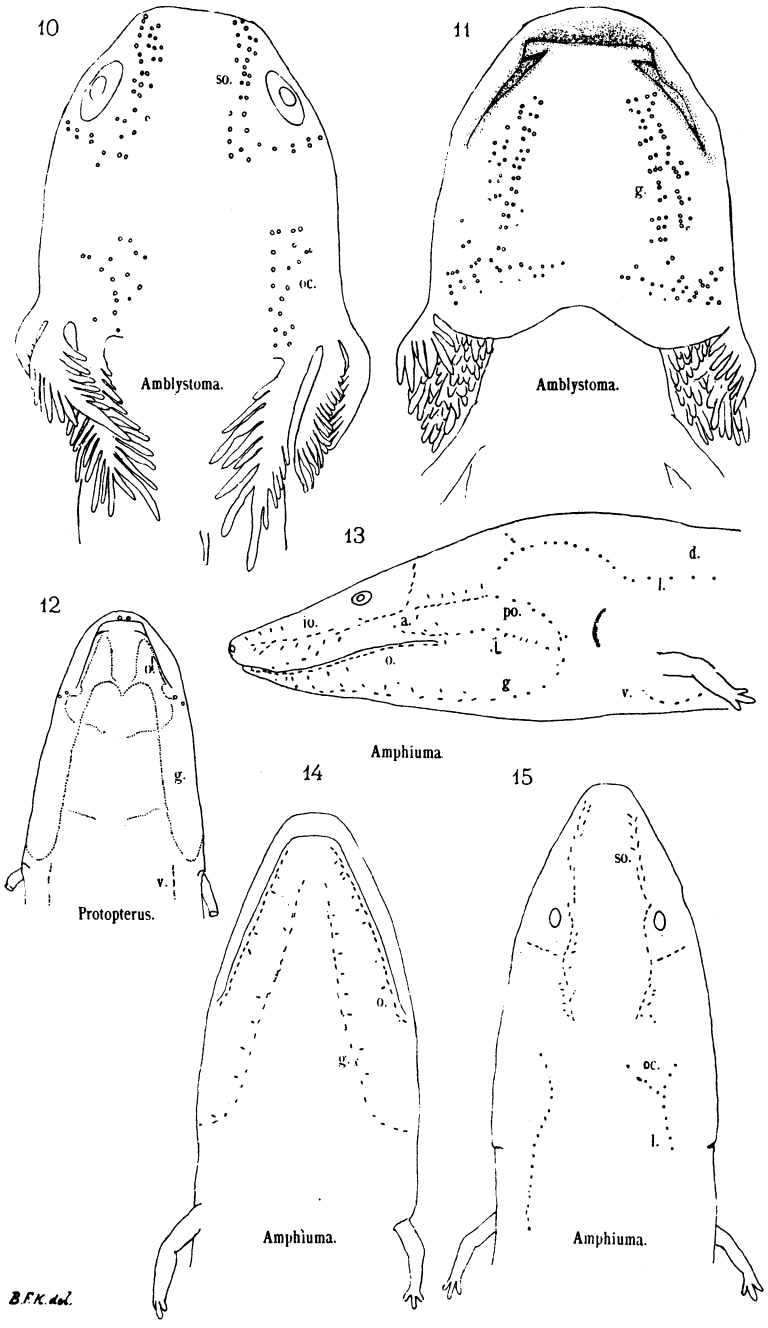
*Protopterus annectens.*

FIG. 12. Specimen 26 cm. long. Ventral aspect of the head, × 1. The circles represent pores of the canals, the free lines of sense organs being indicated by dotted lines.

*Amphiuma means.*

FIG. 13. Lateral aspect of the head, × 1.
FIG. 14. Ventral aspect of the head, × 1.
FIG. 15. Dorsal aspect of the head, × 1.

# PLATE II.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B.F.K. del.

## PLATE III.

FIG. 16. Adult *Necturus maculatus*. Lateral aspect of body. The organs upon the head are omitted, × ½.

FIG. 17. Larval *Amblystoma punctatum*,' 28.5 mm. long. Lateral aspect of the body. × 4.

FIG. 18. Larva of *Gyrinophilus porphyriticus*. Lateral aspect of the body, × 1.

FIG. 19. Larva of *Amblystoma punctatum* 16 mm. long. Lateral aspect, × 8.

### *Diemyctylus viridescens*.

FIG. 20. Adult male. Lateral aspect, × 1.

FIG. 21. Same. Ventral aspect, × 1.

FIG. 22. Same. Dorsal aspect of the head, × 1.

FIG. 23. Larva 32 mm. long. Dorsal aspect of the head, × 8.

### *Gyrinophilus porphyriticus*.

FIG. 24. Larva 82 mm. long. Dorsal aspect of the head, × 2.

FIG. 25. Same. Lateral aspect of the head, × 2.

FIG. 26. Same. Ventral aspect of the head × 2.

### *Protopterus annectens*.

FIG. 27. Lateral aspect of the head, × 1. The circles in this and the two following figures represent pores, the free lines of sense organs being indicated by a dotted line except in Fig. 29.

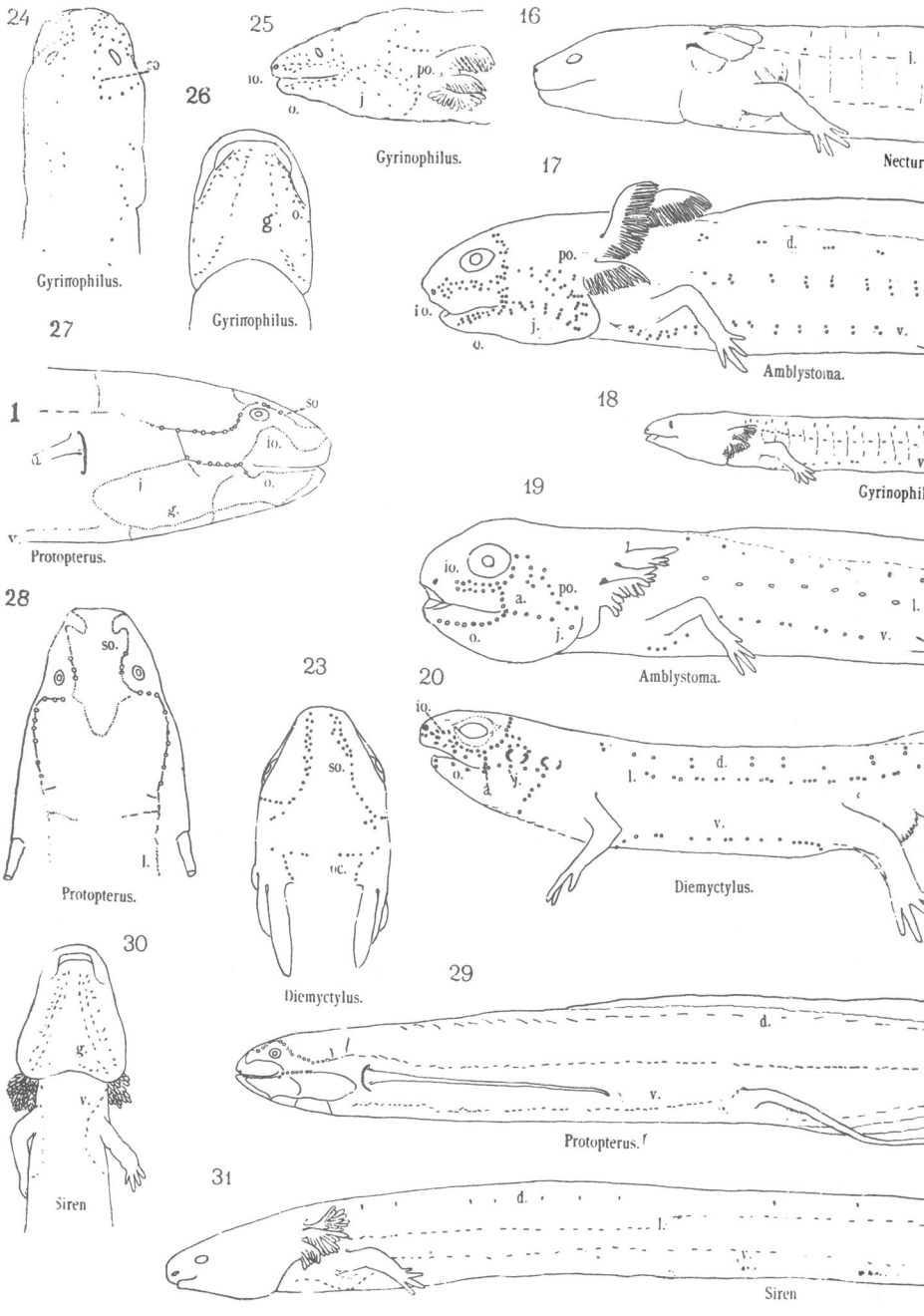
FIG. 28. Dorsal aspect of head, × 1.

FIG. 29. Lateral aspect of the body, × ½.

### *Siren*.

FIG. 30. Ventral aspect of the head, × 1. The short lines indicate groups.

FIG. 31. Lateral aspect of the body, × 1.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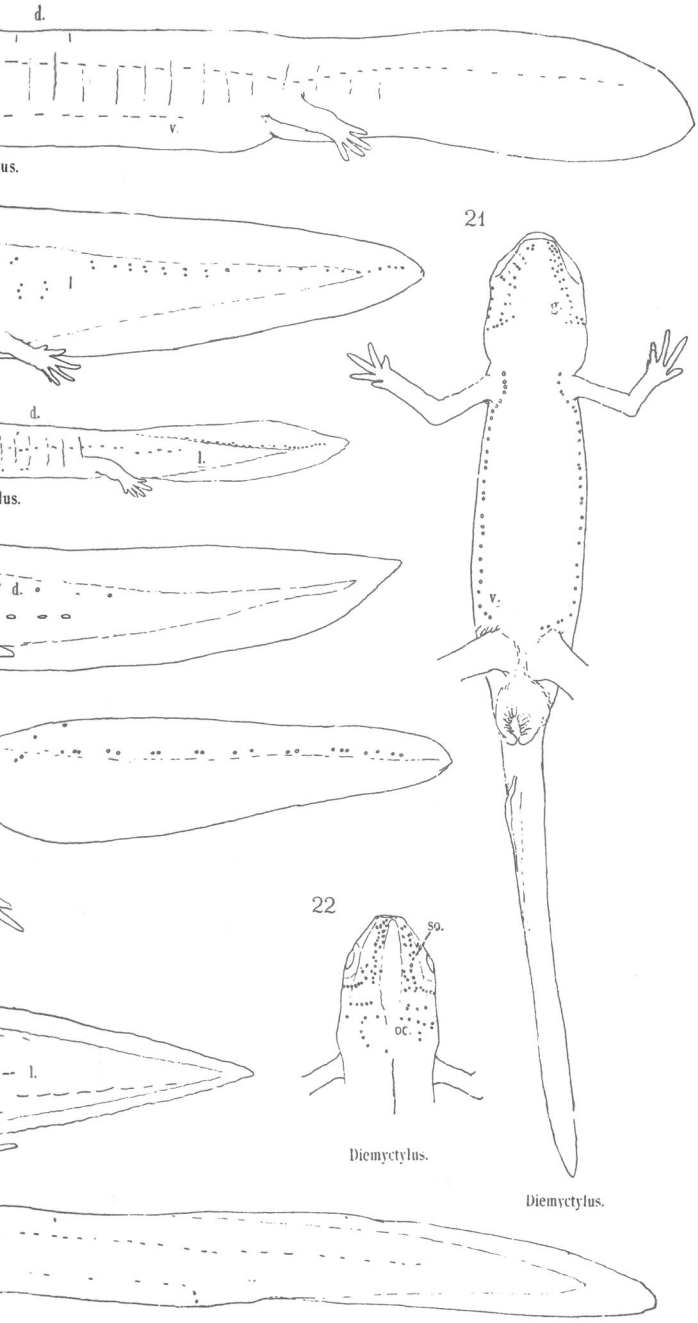
Siren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## PLATE IV.

FIG. 32. A neuromast from the skin of the snout. *Necturus*, × 325.
con.=conical or sensory cells.
sp.=spindle cells.

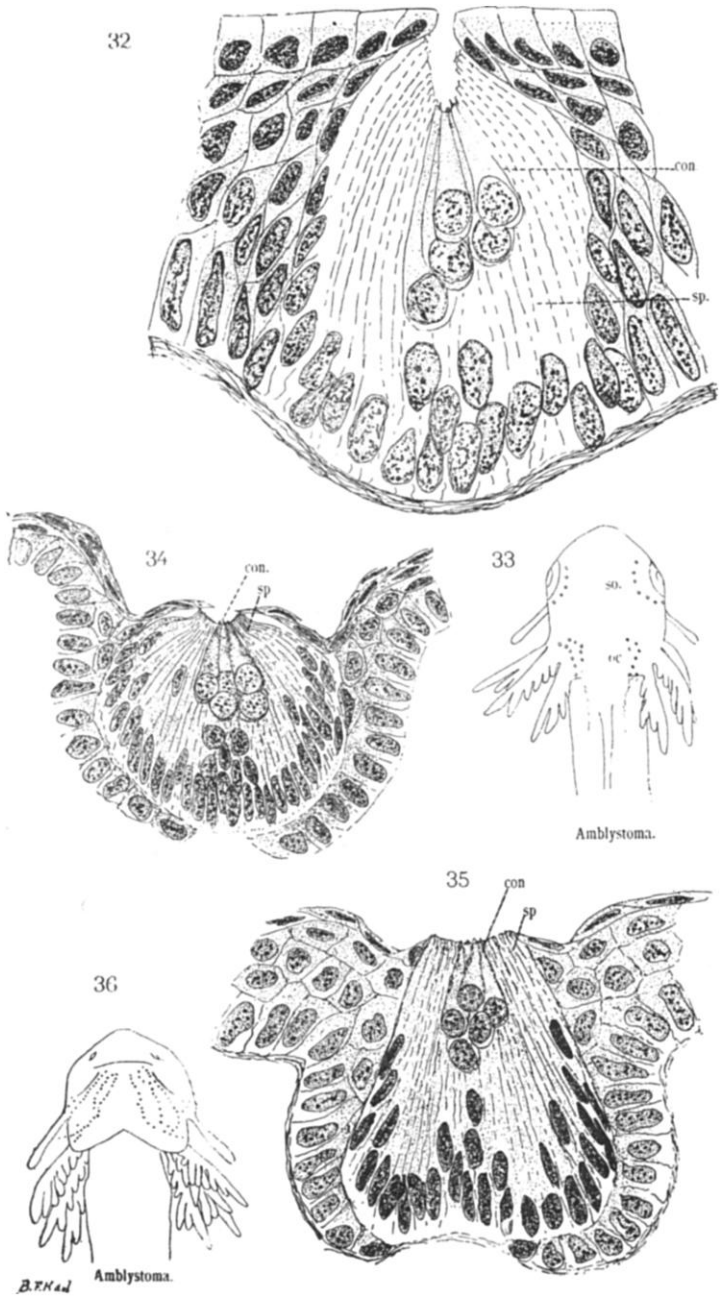
FIG. 33. Larval *Amblystoma punctatum*, arms just budded. Dorsal aspect of the head, × 8.

FIG. 34. A neuromast from the skin of the throat (gular line). *Diemyctylus viridescens*, red (land) form, × 325.
con.=conical cells.
sp.=spindle cells.

FIG. 35. A neuromast from the lateral line near the level of the hind legs. *Diemyctylus viridescens*, adult viridescent (aquatic) form.
con.=conical cells, × 325.
sp.=spindle cells.

FIG. 36. Larval *Amblystoma punctatum*, arms just budded. Ventral aspect of the head, × 8.

# PLATE IV.



## PLATE V.

### *Rana catesbiana.*

FIG. 37. Latero-dorsal aspect of the body, × 2. Short lines indicate groups.

FIG. 38. Ventral aspect of the head, × 2.

### *Cryptobranchus allegheniensis.*

FIG. 39. Ventral aspect of the head, × ½.

FIG. 40. Diagram of the elongated papilla divided by the opening of the sense organs, with a line beneath to show its representation in Fig. 39.

FIGS. 41 and 42. Isolated cells of the neuromasts from the head of *Diemyctylus viridescens*, × 615. Isolated by twenty hours' maceration in one-half Müller's fluid.

### *Lepidosiren paradoxa.*

FIG. 43. Lateral aspect of the head, × ½.

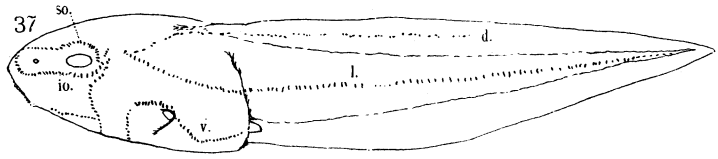
FIG. 44. Dorsal aspect of the head, × ½

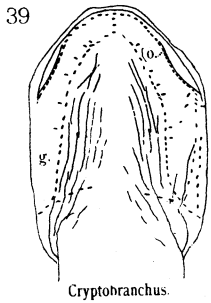
The lines or portions of lines seen are represented in the last two figures by a succession of dots. From the condition of the specimen the plottings were necessarily imperfect.

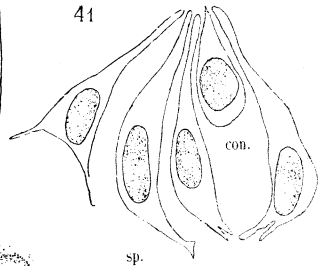
FIG. 45. Two submerged (developing) organs from the skin of *Amblystoma* parotid region, representing apparently an organ dividing by fission, 325.

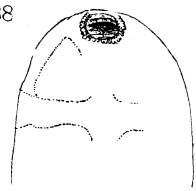
con.=conical cells.

# PLATE V.

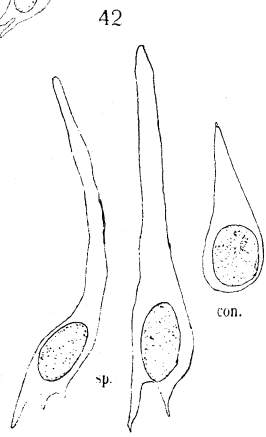


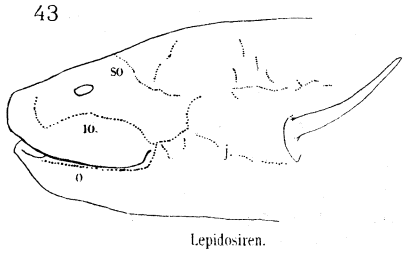



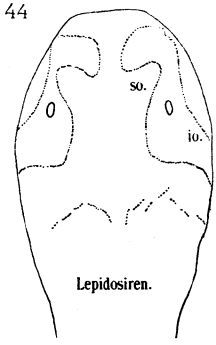









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